

Sweeper Tentacles in a Gorgonian Octocoral: Morphological Modifications for Interference Competition

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Abstract. Elongate tentacles serve an agonistic function in sea anemones and scleractinian corals. Although certain octocorals (soft corals: Octocorallia: Aleyonacea) produce and exude allelochemicals that damage neighboring scleractinian corals, no specialized structures used in agonistic behavior have previously been identified in this large cnidarian subclass. Here, we describe the first evidence of the occurrence and use of specialized agonistic structures, sweeper tentacles, in an octocoral. The encrusting gorgonian *Erythropodium caribaeorum* Pallas (Octocorallia: Gorgonacea) is abundant on shallow reefs in the Caribbean, and competes for space with numerous coral species, sea anemones, and other cnidarians. Zones of contact between this gorgonian and several coral species were observed and recent damage to the coral colonies was noted. Furthermore, the gorgonian develops fields of modified polyps along such borders. These polyps have elongate tentacles termed 'sweeper tentacles,' as in scleractinian corals. Such tentacles lack the side branches (pinnules) characteristic of octocorals in general, and bear a bulbous tip (acrosphere) densely packed with nematocysts. Transplant experiments showed damage to corals placed in contact with the gorgonian's sweeper tentacles and sweeper tentacles were induced when scleractinian corals contacted *Erythropodium* colony borders having exclusively normal tentacles. Thus, sweeper tentacles may contribute to the competitive success of this species in habitats where space is limiting and where there are a number of competing species, many with agonistic mechanisms of their own.

Introduction

Anthozoan coelenterates are important and abundant members of benthic marine communities from the arctic

sublittoral to the extensive tropical coral reefs of the world. As sessile or sedentary animals with little or no ability to move, such species compete with each other and with members of other phyla for substratum on which to grow. Specialized structures and behaviors used in agonistic encounters were first identified in sea anemones from temperate rocky intertidal habitats. Species such as certain *Actinia* and *Anthopleura* (family Actiniidae) use inflated sacks protruding from below the tentacles, the acrorhagi, to damage neighboring individuals of the same or of other species (Abel, 1954; Bonnin, 1964; Francis, 1973; Williams, 1978; Sebens, 1984). This contact results in tissue necrosis where peels of ectoderm, filled with holotrichous nematocysts, adhere to the affected individual. Anemones forming clonal aggregations asexually show a specialization of function: edge individuals put more energy into producing and using acrorhagi than do center individuals, but forego sexual reproduction (Francis, 1976). There is typically a distinct size advantage when individuals compete in this manner, with the loser, usually the smaller individual, moving away from the region of encounter (Brace and Pavey, 1978; Brace, 1981; Ayre, 1982).

Scleractinian corals, including those species responsible for coral reef formation, compete for space either by direct overgrowth or by one of at least two specific agonistic mechanisms (reviewed by Lang, 1984; Lang and Chornesky, 1988). The first mechanism recognized was termed 'extra-coelenteric digestion' and is triggered when corals of two different species grow into contact (Lang, 1973). One of the species exudes mesenterial filaments, the coral's digestive organs, through the mouth or body wall and onto a neighbor's surface. Digestion of the neighbor's tissues takes place *in situ* resulting in a zone of naked coral skeleton that can then be overgrown. Coral species can be ranked in a clear dominance hierar-

chy (Lang, 1973) although a number of ecological factors also affect the outcome of competition by this method (Sheppard, 1979, 1982a, b, 1985; Wellington, 1980; Bak *et al.*, 1982; Logan, 1984, 1985).

A second mechanism of competition was identified for corals a few years later, the development of 'sweeper tentacles' (den Hartog, 1977; Richardson *et al.*, 1979; Wellington, 1980). Sweeper tentacles differentiate in response to several weeks of contact with corals of other species (Chornesky, 1983; Hidaka, 1985; Hidaka and Yamazoto, 1984; Hidaka and Miyazaki, 1984; Hidaka *et al.*, 1987) and can reach five to ten times the length of normal feeding tentacles, thus 'sweeping' an area adjacent to the coral border and causing tissue necrosis in neighboring polyps after contact. Elongate polyps on colonies of *Goniopora* (Sheppard, 1979, 1982b) may perform a similar function and are termed 'sweeper polyps.'

Anemone species in certain families (*e.g.*, Metridiidae) also use elongate tentacles for agonistic behavior. The 'catch tentacle' or 'fighting tentacle' is a longer and often thickened version of one of the feeding tentacles that can be induced to form by contact with genetically distinct conspecifics or with individuals of other species (Williams, 1975, 1980; Purcell, 1977; Watson and Mariscal, 1983; Fukui, 1986). The tip of this tentacle adheres to another individual contacted breaking off and causing tissue damage where it sticks. The agonistic function of these specialized tentacles is clear, resulting in clonal aggregations with spacing between neighboring clones, although habituation (Purcell and Kitting, 1982) and opposite sex tolerance (Kaplan, 1983) may allow for mingling of some clones.

Octocorals, another dominant group of benthic cnidarians, account for much of the biomass and species diversity on coral reefs as well as in steeply sloping deep sea habitats. Caribbean reefs support numerous species of gorgonians, most of which grow as upright branched colonies. Pacific reefs, on the other hand, lack abundant gorgonians but have numerous Alcyonacean octocorals, commonly termed soft-corals, filling similar roles. Octocorals show tissue rejection responses and cytotoxic effects, potential intraspecific competitive mechanisms, in transplant experiments (Theodor, 1970, 1976; Theodor and Senelar, 1975; Bigger and Runyan, 1979). Recent research has demonstrated that certain soft-corals also produce allelochemicals toxic to nearby scleractinian corals and to other soft-corals (Coll *et al.*, 1982; Sammarco *et al.*, 1983, 1985; LaBarre *et al.*, 1986). This competitive mechanism, as well as direct overgrowth, may account for the abundance of soft-corals in some shallow reef areas of the Pacific. However, soft-corals are susceptible to the agonistic mechanisms of scleractinian corals, and often show damage where such encounters occur (Sammarco *et al.*, 1985; LaBarre *et al.*, 1986). Octocorals were not previously known to develop special-

ized structures used in agonistic encounters. Elongate tentacles have been observed on several species of Gorgonacea and an Alcyonacea (several genera, Muzik, 1983, *T. reesii*, F. Bayer, pers. comm.), although potential agonistic use has not been tested.

Erythropodium caribaeorum Pallas, an encrusting gorgonian octocoral, is common on coral reefs throughout the Caribbean. It is the only gorgonian in this region that never produces upright processes but instead forms thin mat-like colonies overgrowing many other species which they contact. Large colonies are particularly abundant in surf-zone and shallow reef habitats (Karlson, 1980, 1983; Sebens, 1982) where the low colony profile may provide some protection from storm-induced damage. Observations of modified tentacles along edges of this species in contact with corals and other neighbors prompted our study of these structures and their function.

Materials and Methods

Surveys of sweeper tentacle occurrence were conducted in shallow back reef and fore reef habitats at Discovery Bay, Jamaica (March 1988), using snorkeling and SCUBA. Following a depth contour and proceeding in a predetermined direction, boundaries of all *Erythropodium* colonies encountered were examined for contact with other cnidarians. Linear measurements were made of each border where contact occurred. Both neighbors were examined for the presence of damaged areas and for specialized structures (sweeper tentacles, acrorhagi), although sweepers were frequently not visible in contracted colonies of *Erythropodium* and most coral species. Damaged areas were characterized by pallid tissue or denuded coral skeleton. If sweeper tentacles were noticed along a border with a non-cnidarian neighbor, that border was also measured and the condition of the neighbor noted.

Two series of transplant experiments were conducted over a 14 month period in the back-reef at Columbus Park, Discovery Bay, Jamaica (1–4 m depth). In each series, 16–18 large *Erythropodium* colonies were mapped and tagged. Branches or plates of the two corals most common in this habitat, *Madracis mirabilis* and *Agaricia agaricites*, were transplanted next to gorgonian colony edges; eight to ten corals were placed in zones without sweeper tentacles and the same number were placed into zones with obvious sweepers. Coral pieces were taken from large aggregations of branches or plates and were removed such that minimal living tissue areas were damaged. Transplants were positioned with tissues in close proximity but actual contact of the coral skeleton with the octocoral colony surface was minimized. Transplants were fixed in place using underwater epoxy (Pettit Co.), keeping the epoxy away from living surfaces of ei-

ther the transplant or *Erythropodium*. The side of each coral away from contact was the control for the transplant process. A few colonies damaged during transplantation, possibly by inadvertent contact with epoxy, showed generalized necrosis over large areas of the colony in subsequent days to weeks and were omitted (<10 percent of transplants). Another 16 gorgonian colony edges without sweeper tentacles were designated as non-transplant controls for spontaneous sweeper tentacle formation by the gorgonian in regions without cnidarian neighbors.

The initial transplant experiments began in February 1987. A second set was initiated in February 1988. All transplants were examined over the first three days then at 5, 12, and 19 days for signs of new damage (white patches or peeling tissue) and for sweeper tentacle formation on either the corals or on the gorgonian. Night time observations were also made several times during the experiment. Damage was recorded as present or absent; in instances of sweeper tentacle induction, the number of modified polyps was recorded. In July 1987 and January 1988 the initial transplants were examined for evidence of overgrowth by either neighbor.

Results

In February 1986 we noticed extensive recent damage to coral colonies adjacent to *Erythropodium* in Discovery Bay, Jamaica (Fig. 1). Close-up photographs of these borders revealed polyps distinct from the normal polyps present on the rest of the *Erythropodium* colony. Normal polyps have eight tentacles of variable length, to approximately 2 cm, with numerous short side branches (pinnules) along their entire length. These tentacles are light to dark brown as a result of abundant symbiotic algae (zooxanthellae) in gastrodermal tissues. The modified tentacles, which we term 'sweeper tentacles' as in the scleractinian corals, were over three times as long as normal tentacles, lacked pinnules, were white to very light brown in color, and had a bulbous tip (acrosphere) (Fig. 2). All eight tentacles of modified polyps generally were of the 'sweeper' form although intermediate forms, where the proximal portion was pinnate and the distal was not, were also common. An extensive survey conducted in 1987 showed that most corals in contact with *Erythropodium* tentacles showed recent damage; almost all such damage was associated with the presence of sweeper tentacles (Table I).

Sweeper tentacles were observed in contact with a number of coral species, several sea anemone species, and a few other non-cnidarian organisms (Table I). Visible damage was observed only on the scleractinian corals which lack the ability to move away from the site of sweeper tentacle formation. Sea anemones are much more mobile and may be able to avoid damage either by

movement or by postural changes. Either event can result in a gain of space for the gorgonian without extensive damage or death of the anemone. Sweeper tentacles appeared to be restricted to the edges near the zone of contact, although polyps one or more centimeters from the edge bore sweepers. Sweepers were never observed scattered over the colony far from the site of contact, as occurs in some scleractinians (Chornesky and Williams, 1983). One non-enidarian group observed frequently in contact with *Erythropodium* borders bearing sweeper tentacles were crustose red algae (several undetermined species). At first we were skeptical that these algae were the only macroorganisms in contact along such borders. Small hydroids or other invertebrates could be present and hard to see, and might be the cause of the sweeper tentacle formation. However, subsequent detailed examination of several such borders and collected specimens observed in the laboratory convinced us that the algae were the only macroscopic occupants of such zones; yet they did not show obvious damage when adjacent to sweepers.

The series of transplant experiments replicated over two years (Table II, III) confirmed the agonistic function of this gorgonian's sweeper tentacles. Corals transplanted into contact with sweeper tentacles showed damage within a few days to a week. Corals transplanted into contact with *Erythropodium* borders with only normal tentacles showed few instances of damage until several weeks had passed. Furthermore, sweeper tentacles were observed in the latter transplant experiments after approximately three weeks of contact, demonstrating that contact with scleractinian corals can induce the formation of these modified structures in *Erythropodium*. Contingency table analyses of these experimental results are given in Tables II and III. Experiments begun in February 1987 were observed again in July 1987 and in January 1988. Although storms had dislodged many of the transplanted corals, of those that survived, all had been partially overgrown by *Erythropodium*. *Madracis mirabilis* developed sweeper tentacles along edges of contact with *Erythropodium* in three of the six surviving transplants, although damage to the *Erythropodium* was not obvious. We did not observe sweeper tentacle formation by *Agaricia* in the three week studies. The few colonies that survived five and eleven months were not examined at night when these tentacles are usually extended. Chornesky (1983) reports that *A. agaricites* did develop sweeper tentacles following prolonged contact with *Erythropodium*.

Sweeper tentacles differ structurally from normal tentacles in several ways (Fig. 3). First, pinnules are absent in sweeper tentacles, but can be seen in reduced form on nearby tentacles that appear intermediate between normal and sweeper tentacles, probably a transitional stage in their development. Several normal and sweeper tenta-



Figure 1. Damaged coral *Agaricia agaricites* adjacent to *Erythropodium* with sweeper tentacles at Discovery Bay, Jamaica, 4 m depth. Scale approximately 6 cm across photograph.

cles were examined at $400\times$ using a compound microscope after relaxing them in 7.5% $MgCl_2$ mixed 50:50 with seawater at room temperature. The gastrodermal layer contained far fewer zooxanthellae in the sweeper tentacles, approximately 86–356 cells per mm relaxed tentacle length *versus* 520–896 cells per mm in normal tentacles ($n = 3$ each). The epidermal layer of the normal tentacles had few nematocysts, approximately 30–50 nematocysts over an entire tentacle surface ($n = 3$), whereas sweeper tentacles had a thickened epidermis composed primarily of nematocysts and cnidoblasts (nematocyst forming cells). These were present by the hundreds and were too numerous to count in fresh preparations. The tip of a normal tentacle bears a small swelling, sometimes with a cluster of nematocysts, sometimes with very few. Sweeper tentacles form a bulbous tip (acrosphere) two to three times the diameter of the normal tentacle tip. The epidermal layer of the acrosphere is packed with nematocysts several layers deep. A fraction ($<20\%$) of normal tentacles have an acrosphere as well; these may be intermediate forms developing into sweepers. It is likely that both the acrosphere and the epidermis along the entire sweeper tentacle length are involved in causing damage

to neighboring cnidarians. All eight tentacles of each modified polyp become sweeper tentacles, and there appears to be some modification of the polyp itself as well, although it does not greatly elongate. Also, spicules of these polyps were clear compared to the deep red color of spicules in normal polyps.

Discussion

This study identified agonistic structures in the subclass Octocorallia, a modified polyp and tentacles that serve an agonistic function in competition for space with other anthozoan cnidarians and possibly with non-cnidarian space competitors as well. The sweeper tentacles of *Erythropodium* are much more numerous and extensive than sweeper tentacles we have observed on scleractinian corals. Fields of sweeper tentacles (8 per polyp) on hundreds of polyps were common along edges in contact with both corals and anemones. These sweeper tentacles are able to kill tissue of adjacent scleractinians, potentially enabling *Erythropodium* to subsequently overgrow the denuded coral skeleton, an advance which may not have been possible while the coral edge was still alive. It



Figure 2. A. Sweeper tentacles of *Erythropodium* extended *in situ*. Scale approximately 2.2 cm across photograph. B. Normal pinnate tentacles, scale approximately 1.7 cm across photograph (Discovery Bay, Jamaica, 3 m depth).

Table I

Survey of interactions along *Erythropodium* borders

Species	Total	With sweepers			Without sweepers		
		N (S)	Dam	Length (cm, \pm S.D.)	N	Dam	Length (cm \pm S.D.)
<i>Agaricia agaricites</i>	37	28	26	5.6 \pm 3.1	9	1	3.1 \pm 2.9
<i>Briareum asbestinum</i>	14	0	0	—	14	0	2.5 \pm 1.2
<i>Condylactis gigantea</i>	5	3	0	6.7 \pm 2.9	2	0	16.0 \pm 5.7
<i>E. caribaeorum</i>	7	7	0	4.4 \pm 2.9	0	0	—
<i>Heteractis lucida</i>	35	28	0	11.2 \pm 6.6	7	0	7.7 \pm 2.2
<i>Palythoa caribaeorum</i>	6	0	0	—	6	0	4.2 \pm 3.1
<i>Porites astrooides</i>	3	1	1	—	2	1	4.5 \pm 0.7
Red crustose algae	52	52	0	2.9 \pm 1.2	0	0	—

Surveys of *Erythropodium* borders (1987), noting the condition of neighboring cnidarian colonies or individuals (damaged or not), and the presence of sweeper tentacles on *Erythropodium*. Instances where sweeper tentacles were observed adjacent to non-cnidarian neighbors are also noted. Additional observations of sweeper tentacles and damage to adjacent colonies are given for other colonies examined, but which were not part of the systematic survey. Number of observations in parentheses. N = number of contacts, N (S) = number of contacts with sweeper tentacles on *Erythropodium*, Dam = number of cases where neighbor was damaged, length = mean length of border, S.D. = standard deviation.

Other borders with sweepers on *Erythropodium*. Corals: *A. agaricites* (5); *Diploria strigosa* (1); *Eusmilia fastigiata* (1); *Favia fragum* (1); *Madracis mirabilis* (2); *Meandrina meandrites* (2); *Montastrea annularis* (1); *M. cavernosa* (3); *Mycetophyllia* sp. (1); *P. astrooides* (6); *Porites furcata* (1); *Porites porites* (1); *Siderastrea siderea* (2); Anemones: *Aiptasia tagetes* (1); *Bartholomea annulata* (1); *H. lucida* (7); *Lebrunia danae* (1); *Telmatactis* sp. (2); Hydrozoa: *Millepora alvicornis* (3); *M. complanata* (4); unidentified hydroid (2); Sponges: *Cliona* sp. (1); *Iotrochota birotulata* (2); unid. green demosponge (1); Others: *didemnid* ascidian (1); *E. caribaeorum* (3); *P. caribaeorum*, zoanthid (5); *Paradisicosoma neglecta*, corallimorpharian (1); *Zoanthus solanderi*, zoanthid (1); algal mat (1).

Table II

Results of transplant experiments of corals into contact with *Erythropodium* (1987 series)

	Initial N	Week 1 (5 days)			Week 3 (19 days)		
		N	Dam	N (S)	N	Dam	N (S)
<i>Erythropodium</i> with							
<i>Madracis mirabilis</i>							
Edges with sweepers	10	8	6	—	6	6	—
opp. side controls	10	8	0	—	7	0	—
Edges without sweepers	10	8	2	0	7	2	2 (6, 5)
opp. side controls	10	8	0	—	6	0	—
Non-transplant controls	10	8	—	0	7	—	0
<i>Erythropodium</i> with							
<i>Agaricia agaricites</i>							
Edges with sweepers	8	8	5	—	8	8	—
opp. side controls	8	8	0	—	8	0	—
Edges without sweepers	8	8	3	0	8	7	4 (8, 3, 8, 10)
opp. side controls	8	8	0	—	8	0	—
Non-transplant controls	8	8	—	0	8	—	0

Results of 1987 transplant experiments at Columbus Park, Discovery Bay, Jamaica. Small plates or branches of the two most common coral species in this habitat, *Madracis mirabilis* and *Agaricia agaricites*, were transplanted into contact with *Erythropodium* edges initially with and without sweeper tentacles. N = number of surviving transplants, Dam = number with damage to corals in contact region, N (S) = number of edges with sweeper tentacles on *Erythropodium*. Numbers in parentheses are counts of polyps with newly developed sweeper tentacles along each edge where they developed during the experiment.

G-test for independence (with Yates' correction) show significantly greater occurrence of damage next to sweeper tentacles than occurred on opposite sides of transplanted corals (opp. side controls, $G = 8.2$ ($P < 0.005$) at 5 days; $G = 11.9$, ($P < 0.005$) at 19 days for *M. mirabilis*. $G = 5.1$, ($P < 0.05$) at 5 days; $G = 14.7$, ($P < 0.005$) at 19 days for *A. agaricites*.) Damage next to edges without sweepers was not significant after 5 days for either species compared to opp. side controls, but was significant for *A. agaricites* after 19 days, $G = 11.2$, ($P < 0.005$). Damage frequency at edges with sweepers differed significantly from that at edges without sweepers for *M. mirabilis* only at 19 days, $G = 4.8$ ($P < 0.05$).

Table III

Results of transplant experiments of corals into contact with *Erythropodium* (1988 series)

	Initial N	Week 1 (4-5 days)			Week 3 (19 days)		
		N	Dam	N(S)	N	Dam	N(S)
<i>Erythropodium</i> with <i>Madracis mirabilis</i>							
Edges with sweepers	12	8	4	—	6	5	—
opp. side controls	12	8	0	—	6	0	—
Edges without sweepers	13	11	1	0	6	1	2 (2, 3)
opp. side controls	13	11	0	—	6	0	—
Non-transplant controls	13	13	—	0	13	—	0
<i>Erythropodium</i> with <i>Agaricia agaricites</i>							
Edges with sweepers	14	13	12	—	8	6	—
opp. side controls	14	13	0	—	8	0	—
Edges without sweepers	14	14	2	0	13	6	7 (10, 4, 3, 4, 5, >10, >10)
opp. side controls	14	14	0	—	13	0	—
Non-transplant controls	14	14	—	0	13	—	0

Results of 1988 transplant experiments of corals into contact with *Erythropodium*. Abbreviations same as Table 1.

G-tests for independence (with Yates' correction) show significantly greater occurrence of damage next to sweeper tentacles than occurred on opposite sides of transplanted corals (opp. side controls: not sig. at 5 days, $G = 6.12$, ($P < 0.025$) at 19 days for *M. mirabilis*, $G = 22.4$, ($P < 0.005$) at 5 days, $G = 7.46$ ($P < 0.01$) at 19 days for *A. agaricites*). Damage next to edges without sweepers was not significant versus opposite side controls after 5 days for either species but was significant for *A. agaricites* after 19 days, $G = 6.16$, ($P < 0.025$). Damage frequency at edges with sweepers differed significantly from that at edges without sweepers for *A. agaricites* only at 5 days, $G = 14.94$ ($P < 0.005$) and not for *M. mirabilis* at either time.

is interesting that these structures were discovered in the only completely encrusting gorgonian species in the Caribbean; the encrusting habit brings the growing edges and tentacles into frequent contact with other competitors for primary space. The upright habit of other gorgonians allows them to avoid most such space competition on the primary substratum, although certain other upright enidarian species, such as fire-corals (*Millepora* spp.), attack and take space from erect gorgonians then use the denuded gorgonian axis as substratum (Wahle, 1980).

Erythropodium is a common enidarian on shallow Caribbean reefs, yet its ecology is poorly understood. It is avoided by most fish and invertebrate predators (Sebens, 1982) and contains potent toxins effective at least against vertebrate predators (Pawlik *et al.*, 1987). However, J. D. Witman (unpub. data) reports numerous observations of feeding on *Erythropodium* by the predatory gastropod *Cyphoma gibbosum* and Karlson (1983) notes predation by the sea urchin *Diadema antillarum* and by the fire-worm *Hermodice carunculata*. In shallow habitats just behind the reef crest at Discovery Bay, Karlson (1980) observed *Erythropodium* overgrowing the zoanthids *Zoanthus solanderi* and *Palythoa caribaeorum* and the corals *Porites astreoides*, *P. porites*, *Agaricia agaricites*, *Siderastrea siderea*, and *Acropora palmata*, accounting for 73% of 37 mapped overgrowth interactions at his study site. *Erythropodium* also is an aggressive competitor for space in Lameshur Bay, St. John, U.S.V.I., where

it overgrew four scleractinian species, two hydrocoral species, one zoanthid, an ahermatypic coral, and nine sponge species in quadrats monitored for two years (J. Witman, unpub. data, photographic monitoring of 32 0.25 m² quadrats at 6 m and 13 m depth, 1985-1987).

In our experiments, *Erythropodium* damaged and overgrew two coral species that are abundant on the same shallow reefs. Observations and surveys indicate that *Erythropodium* is a successful space competitor compared to most other coral species as well, based on incidence of damage and edge overlap. However, because of its non-rigid structure, it is difficult to tell whether any corals have damaged or taken space from *Erythropodium*. Certain edges in contact with corals and anemones were pale in color with widely spaced polyps, many of which remained retracted while all other polyps on the colony were fully expanded. It is possible that such zones represent areas where the colony has been injured and is retreating, resorbing tissue, and thus losing space to a superior competitor.

Sweeper tentacles of *Erythropodium* were observed frequently in contact with crustose red algae. All previous studies of enidarian agonistic behaviors suggest that these behaviors are effective only against other enidarians, except for studies in which algal growth was reduced in zones of contact with anthozoan tentacles (Bak and Borsboom, 1984; DeRuyter van Stevenink *et al.*, 1988). Reduced algal colonization also was noted in

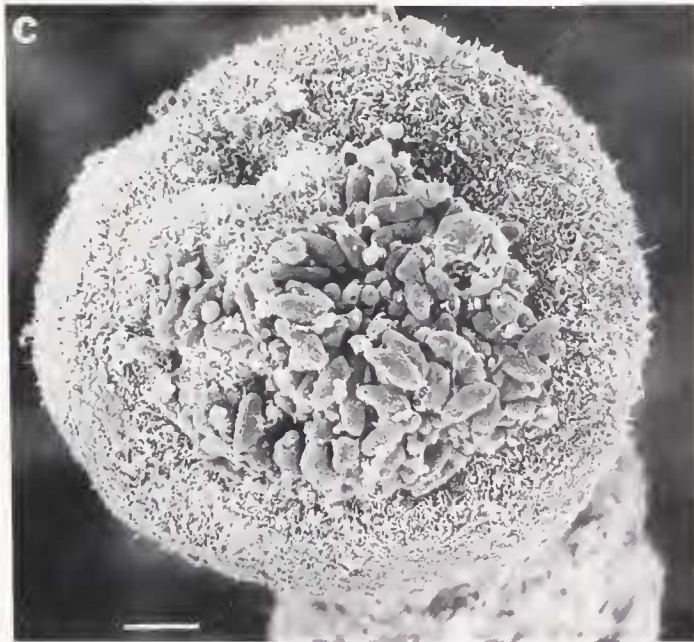
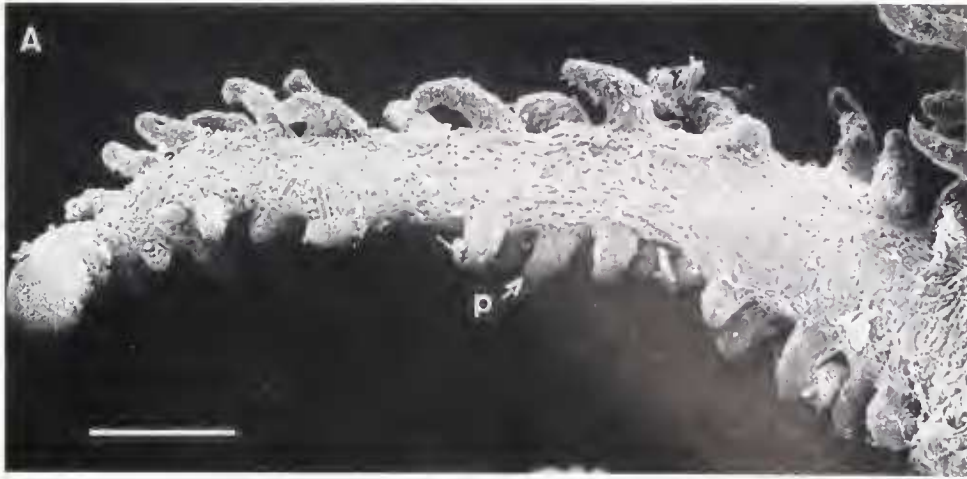


Figure 3. Scanning electron micrographs of normal (A) and sweeper (B) tentacles of *Erythropodium*. Note the absence of side branches (pinnules, P) on the sweeper tentacle and the knobbed tip (acrosphere) on both tentacles. Scale bars 100 μm in A, B. (C) Enlarged view of acrosphere from a sweeper tentacle with a central cluster of large nematocysts. Scale bar 10 μm .

scraped patches within a Pothid bed (Sebens, 1982). Results such as these indicate that anthozoan mucus or nematocysts may have negative effects on adjacent algae and provide a possible explanation of why sweeper tentacles might form in response to crustose algae in this case. The need for such defense was illustrated by several observations of partial over growth by shelves of crustose algal thallus that had lifted off the substratum and had partially overgrown edges of corals and of several *Erythropodium* colonies in our study area.

Sweeper tentacles also were noted in several instances where two *Erythropodium* colonies contacted each other with no intervening substratum. Although the evidence is not experimental, it suggests that sweeper tentacles are used intraspecifically as well as interspecifically in this species. Corals also are able to recognize genetically different colonies or colony fragments, resulting in fusion or non-fusion at intraspecific colony borders (Hildeman *et al.*, 1979; reviewed by Lang and Chornesky, 1988). Intraspecific use of sweeper tentacles also has been observed (Sheppard, 1982; Hidaka and Yamazoto, 1984; Sebens, in Lang, 1984), and thus must involve colony genotypic recognition, as in the fusion process.

The development and use of sweeper tentacles is a newly recognized competitive mechanism in the subclass Octocorallia. Although "sweeper tentacles" have been recorded in erect species including *Corallium* (Gorgonacea, Abel, 1970), *Bebryce*, *Cyclomuricea*, *Villogorgia*, and *Acalyegorgia* (Gorgonacea, Muzik, 1983, note photographs), and *Dendronephthya* (Alcyonacea, Muzik, 1983), each was described as a potential feeding structure and none have been demonstrated to have an agonistic function. Such tentacles are held well off the substratum, were not in potential contact with neighboring organisms, and were not devoid of pinnules. Alcyonacean octocorals in Australia produce allelochemicals that can damage adjacent anthozoans (Coll *et al.*, 1982; Sammarco *et al.*, 1983, 1985; LaBarre *et al.*, 1986). However, this competitive mechanism apparently does not rely on specialized structures. The delivery of nematocysts, and their toxins, to the surface of a competitor depends on structures that can span the distance between neighbors. Sweeper tentacles, several times as long as the feeding tentacles, are an obvious way to do this. Similarly, mesenterial filament extrusion by corals delivers both digestive enzymes and nematocysts to a neighbor's surface. Sea anemones with acrorhagi depend on inflation of acrorhagi and on extension and bending of the column to achieve this added reach.

The appearance of sweeper tentacles in relatively few families within three separate orders of the class Anthozoa (Actiniaria, Scleractinia, Gorgonacea) suggests that this competitive mechanism may have evolved independently several times. Tentacles are usually the first part of an anthozoan to contact a neighbor, and they already

contain nematocysts used for feeding and for defense against predators. Therefore, feeding tentacles of edge polyps are a likely structure to develop a competitive or agonistic function. The feeding and defensive functions of tentacles can thus be considered pre-adaptations with regard to competition for space. Alternatively, they may represent a primitive character shared by all three orders but expressed in relatively few families, genera, and species. The discovery of sweeper tentacles in *Erythropodium* should stimulate examination of other gorgonian and alcyonacean species for the presence of similar structures. It may then be possible to determine whether this is a unique adaptation to local conditions in this species, or whether it is a more general phenomenon present in encrusting octocorals from other geographic regions or habitat types as well.

Acknowledgments

We thank R. Aronson and the East/West Program students for field assistance, and the Discovery Bay Marine Laboratory, University of the West Indies, for allowing use of facilities and boats. We also thank W. Fowle, M. P. Morse, and N. W. Riser for assistance with light and electron microscopy techniques, B. L. Thorne and J. Witman for improvements to the manuscript, and L. Chornesky and one other reviewer for many helpful suggestions. This is contribution No. 166 of Northeastern University's Marine Science Center and No. 460 of the Discovery Bay Marine Laboratory, Univ. of the West Indies.

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